

RESOLUTION OF THE RELATIONSHIPS WITHIN THE NORTH AMERICAN PITCHER PLANT GENUS, *SARRACENIA*

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The North American pitcher plants (*Sarracenia*) are arguably one of the most charismatic groups of carnivorous plants and have garnered a great deal of attention for their diversity in trapping structures. The first *Sarracenia* specimen was described as early as 1570, and since then, the relationships among the species have remained an enigma for researchers. Originally, there were several attempts at describing relationships among *Sarracenia* through morphological measures, but with little consensus. The first genetic studies did little to improve our understanding of the relationships within *Sarracenia*, but did identify *Darlingtonia californica* (Cobra Lily) as the most ancient of the Sarraceniaceae family, with *Heliamphora* sharing a recent common ancestor with *Sarracenia* (Albert *et al.* 1992; Bayer *et al.* 1996; Neyland & Merchant 2006). The most recent genetic approach attempted to uncover species relationships using eight genes (Ellison *et al.* 2012). While Ellison *et al.* (2012) provided some resolution within the genus, most species relationships remained a mystery; however, they were able to date the genus to roughly 0.5-3 million years old, which is extremely recent in evolutionary time. In addition, members of the *Sarracenia* genus are prone to rampant hybridization with one another, making it even more difficult to determine the relationships among species.

Building off of these previous studies, we captured 199 genes across the 11 species recognized by Mellichamp and Case (2009) (*alabamensis*, *alata*, *flava*, *jonesii*, *leucophylla*, *minor*, *oreophila*, *psittacina*, *purpurea*, *rosea*, and *rubra*), along with three subspecies/varieties from the *purpurea* complex, two subspecies from the *rubra* complex, one *minor* variety, and two *flava* varieties (Stephens *et al.* 2015). These data were analyzed in a way that takes different genes' history into account, allowing them to elucidate many relationships with the genus (Fig. 1). In accordance with previous genetic attempts, *oreophila*, *alata*, *leucophylla*, and the *rubra* complex are closely related (Ellison *et al.* 2012; Neyland & Merchant 2006). However, the *rubra* complex remains ambiguous, as the relationships of the subspecies are not well supported. Additionally, *alata* does not appear to be a genetically distinct species and may be considered a part of the *rubra* complex. Interestingly, results seem to support the species level designation of *alabamensis* (*rubra* subsp. *alabamensis*) and *jonesii* (*rubra* subsp. *jonesii*), which have important implications regarding their status as endangered species. Both are found in isolated populations (Fig. 2) and are very morphologically different from other members of the *rubra* complex.

Contrary to previous genetic attempts at resolving the relationships within the genus, the *purpurea* complex is not basal to all other *Sarracenia*. Rather, this complex shares a recent common ancestor with *psittacina/flava/minor*. *Sarracenia purpurea* is the most widespread *Sarracenia* species, ranging from the Coastal Plain across Canada (Fig. 2). The complex has generally been divided into two subspecies, with one subspecies having three varieties. These designations are based on geographic distribution (Fig. 2). The results suggest that *purpurea* subsp. *venosa* var. *montana* is the ancestral form of *purpurea*, which has implications for its conservation status. Specifically, this species is under consideration for listing as an endangered taxon by the U.S. Fish and Wildlife Service and the Convention on International Trade in Endangered Species (CITES). The remaining *purpurea* subspecies relationships are less supported. Finally, the relationships found between *minor*, *psittacina*, and *flava* were supported by previous studies (Bayer *et al.* 1996; Neyland & Merchant 2006) with Ellison *et al.* (2012) supporting the sister relationship of *flava* and *psittacina*.

**MP-EST Species tree,
199 nuclear loci**

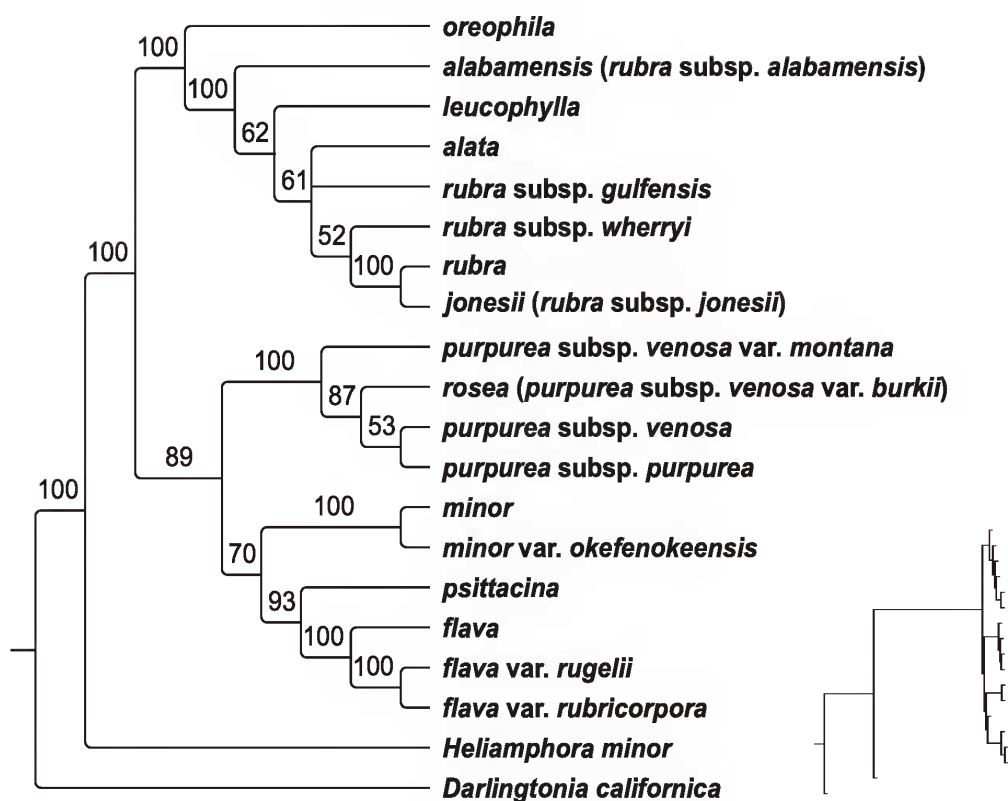


Figure 1: *Sarracenia* species tree based on 199 nuclear genes. Bootstrap support is listed above respective nodes. Bootstraps of >85 are well supported relationships, 70-85 are mildly supported, and <70 are considered weakly supported. Nodes with <50 support are collapsed (i.e. *alata* and *rubra* subsp. *gulfensis*).

This latter relationship is noteworthy, considering that these two species display opposite extremes of pitcher morphology.

In the context of biogeography, some interesting trends emerge. First, *oreophila* and *purpurea* subsp. *venosa* var. *montana* are both found on ancient soils in the Appalachians (Fig. 2). This combined with their placement as the most ancient species in each of their respective groups might suggest that *Sarracenia* ancestors may have originated in that region. This hypothesis may also explain the current geography of descendants of the *oreophila* ancestor (*alabamensis*, *leucophylla*, *alata*, and some *rubra* subspecies) along the Gulf Coastal Plain (Fig. 2), with the idea that descendants gradually migrated down the Apalachicola-Chattahoochee River drainage. Likewise, descendants from the group that are more closely related to *purpurea* subsp. *venosa* var. *montana* (*purpurea* subsp. *venosa*, *purpurea* subsp. *purpurea*, *minor*, *psittacina*, and *flava*) may have migrated down drainages that lead to the Atlantic Coastal Plain (Fig. 2). The other possible scenario is that the descendants from the Appalachians migrated down the Apalachicola-Chattahoochee River drainage and diverged east and west of the drainage. Future work focusing on the population genetics of *Sarracenia* can better elucidate the geographic origin and spread of this group. This is of interest, especially in regard to the *rubra* and *purpurea* complex.

The use of 199 genes has greatly improved our understanding of *Sarracenia* evolution. Resolving these relationships has important implications for conservation especially given the confusion in nomenclature designations (Ellison *et al.* 2014). For example, the listing of *S. rubra* subsp. *ala-*

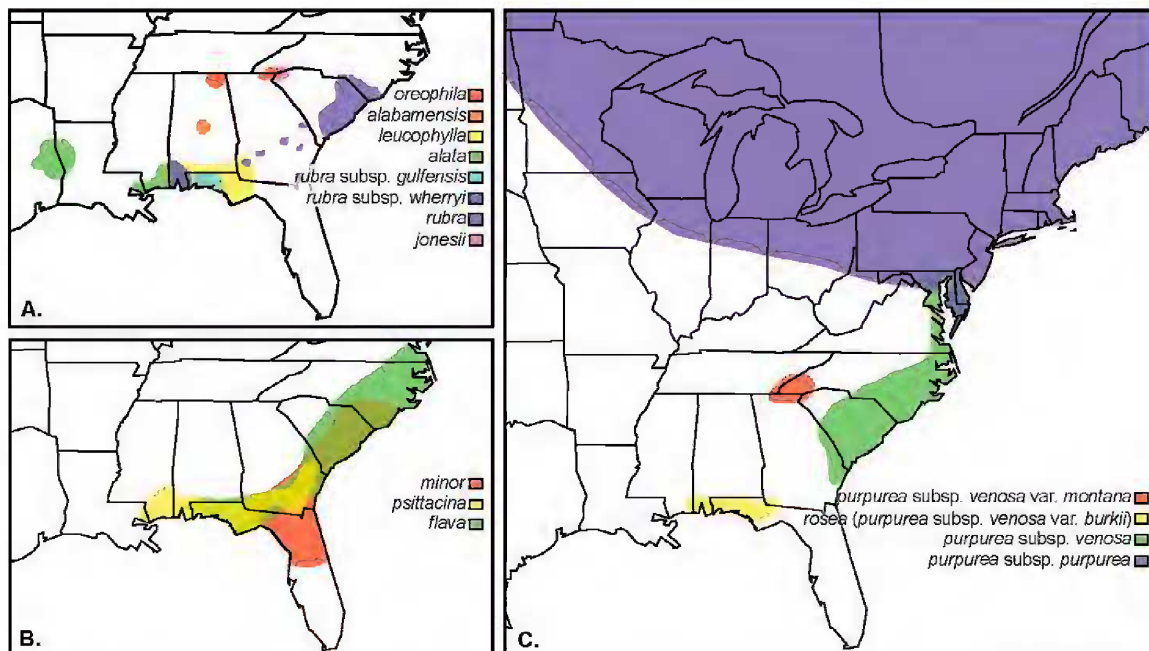


Figure 2: Range maps for *Sarracenia* species. (A) Species and subspecies ranges from the *oreophila* clade. (B) Ranges for the *flava*–*minor*–*psittacina* clade; varieties are not shown. (C) Ranges of the subspecies within the *purpurea* complex.

bamensis to *S. alabamensis* can have profound influences on resources allocated to its conservation. Therefore, an important next step is to reevaluate the nomenclature across the genus in lieu of the resolved evolutionary relationships, with specific emphasis on the *rubra* and *purpurea* complex. This will hopefully lead to less confusion for management and conservation officials that are in charge of protecting these rare and endangered species.

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